

XXII.—On true Parthenogenesis in Plants.

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It would indeed be difficult to find anywhere a more evident proof of the imperfection of human knowledge than is furnished by the contradictory results of the latest embryological investigation, in the departments of zoology as well as of botany. If our knowledge of the process of fecundation in animals appear to have made an important step forward through the observation of the penetration of the spermatozoids into the ovum,—if this seemed to put beyond all doubt the material participation of the spermatozoids in the formation of the embryo,—we must be doubly surprised by the observation, that in particular—apparently determinate—cases, the formation of the embryo occurs without any cooperation of the spermatozoids, therefore *without previous fecundation of the ovum*. This true Parthenogenesis, demonstrated with all the exactness which science can require by Prof. Von Siebold†, in the Lepidoptera, and in the Bees particularly, is paralleled by analogous cases in the neighbouring domain of plants.

In calling the attention of zoologists for a moment to an account of them, I have a twofold purpose: to convince those still in doubt by the number of proofs, and to attract to the subject itself as many observers as possible.

Embryological researches in the vegetable kingdom have kept pace with those in the department of zoology. Analogues of the animal ovum, analogues of the animal fecundating matter, have been demonstrated in all groups of the vegetable kingdom, with the exception of the Fungi and Lichens.

To the ovum corresponds the *germ-vesicle* of the Phanerogamia, of the Rhizocarpeæ, Equisetaceæ, Ferns and Mosses; and, besides this, the *primordial spore-cell* of the Algæ. The germ-vesicle (*vegetable ovum*) presents itself as a perfect cell, furnished with a membrane and a cytoblast‡; in the Algæ we find, instead of the perfect cell, one devoid of a membrane, an *ovum* without an integument,—the naked primordial spore-cell.

To the spermatozoids contained in the spermatic fluid of animals, the material basis of which we must regard, according to

* Translated from Siebold and Kölliker's Zeitschrift, viii. Heft 4 (1857), by Arthur Henfrey, F.R.S. &c.

† True Parthenogenesis in Moths and Bees, &c. By C. Th. Von Siebold. Translated by W. S. Dallas, F.L.S. London, Van Voorst, 1857.

‡ We dissent from the author on this point, believing that the unimpregnated germ-cell has not yet a cellulose membrane, but resembles the unimpregnated spore of *Fucus*. See Annals of Nat. Hist. 2nd ser. xviii. p. 217 (Sept. 1856).—[A. II.]

researches now before us, either in its totality or in part, as the proper fecundating power, as the *actual fecundating substance*,—correspond the *spontaneously moving form-elements* (*spermatozoids*) in the fertilizing (spermatic) fluid of plants. In some Algæ and in the Phanerogamia only are these form-elements wanting in the fecundating fluid; the fertilizing fluid itself appears in these cases as the fecundating substance.

Throughout the vegetable, as in the animal kingdom, the *act of fecundation* is completed by the fecundating matter—whether it possesses an independent form or not—coming into immediate contact with the vegetable ovum and its contents*. This is the case in particular in the Phanerogamia, as I have placed beyond all doubt by my investigations†. As we shall have in the sequel to speak more minutely, and exclusively, of this, it is requisite to sketch briefly the process of fecundation in the Phanerogamia, and in so doing, we may take the liberty, for the sake of simplicity, to omit all reference to the fecundating processes of the Coniferæ and Cycadææ, which deviate from those of the rest of the Phanerogamia in many respects.

The *ovum to be fertilized*, the germ-vesicle, is contained, in the Phanerogamia, in a large cell, the so-called embryo-sac, which itself constitutes the centre of a variously constructed, cellular organ, the *seed-bud* (*gemmula*—hitherto inconveniently termed *ovulum*). This seed-bud (ovule) it is which, when perfectly developed, becomes, in its mature condition, the *seed*. It is enclosed in the germen or ovarium, and usually a number of these ovules occur in the same ovary.

The *fecundating matter* consists of the contents of isolated cells, the *pollen-grains*. If one of these pollen-grains arrive at the proper part of the ovary, upon the *stigma*, it undergoes further development. The cell of which it consists grows, becomes tubular (*pollen-tube*), and penetrates through all the parts lying between the stigma and the embryo-sac, so as at length to allow its contents to pass over into the embryo-sac and germ-vesicle, by endosmose, and thus to render the germ-vesicle capable of further development, of forming an embryo.

It is no wonder, in the face of the observations on the material participation of the fecundating substance in the formation of a new plant (*i. e.*, in the Phanerogamia, the formation of seeds), mentioned at the beginning of this paper, that little faith came to be placed in the accounts of the earlier botanists, of

* For the further explanation of the conditions here referred to, I would direct the reader to my recent treatise “Befruchtungsprocess im Pflanzenreiche,” &c., Leipsic, 1857. [A translation of this will shortly appear in our pages.—Ed. *Ann. Nat. Hist.*]

† Radlkofer. Die Befruchtung der Phanerogamen. Leipsic, 1856.

cases of formation of seed without cooperation of the male organs, of the pollen. The more surprising therefore are the proofs of the reality of such cases which are here gathered from the most recent observers.

In the first rank here must be mentioned the observations on *Cælebogyne ilicifolia*, a diœcious Euphorbiaceous plant, native of Australia, female specimens of which were long since introduced into England, and were widely distributed from there, before the male plant had been detected by travellers in its native country. No living specimens of the male plant have yet reached Europe; only a dried shoot with male flowers exists in the Herbarium at Kew. A glance at this suffices to show, from the composition of the inflorescence of the plants, the impossibility of the occurrence of a hermaphrodite flower in *Cælebogyne*, and to show, further, that if the exceptional case which has been observed in other plants, of a production of male flowers on female specimens of diœcious plants, occurred in *Cælebogyne* also, it could not be overlooked. Finally, all botanists who have had an opportunity of examining the female plants of *Cælebogyne*, and among these are numerous authorities, agree in declaring that no male organs occur on them. In spite, however, of the fact that the exclusion of the fertilizing pollen of the same species must here certainly be most perfect, the plants cultivated at Kew annually ripen an abundance of seeds, from which even the third or fourth generation of (*female*) plants have been raised there.

Observation of the fact that at Kew the *Cælebogyne* is kept in company with other Euphorbiaceæ, led me to think, while staying there, that the enigma might probably find its solution in the detection of a hybridation. Although this conjecture was very much weakened by the simultaneous observation that the progeny have hitherto preserved entirely the character of the original mother-plant, yet I was more inclined even to the idea that, as an exceptional case, a hybrid might be developed with the characters of only one of its parents, than to believe that a seed, and consequently an embryo, could be developed without previous fecundation. I endeavoured to acquire certainty on this point by the following means:—

1. An examination of the stigmas of all the ovaries (placed at my disposal by the kindness of Sir W. Hooker, Director of the Garden), in order to detect if pollen-grains were present; and
2. A search through the cavities of the ovaries and the ovules, for the presence of pollen-tubes.

Among twenty-one ovaries which I examined, I found, upon the stigma of *one* alone, a dried pollen-grain, which adhered to the surface with other bodies which come under the denomina-

tion of dust. No pollen-tube could be observed in this case. It is further to be remarked, that no embryo could be found in the ovules of this ovary, although it was at the proper age.

Each ovary contains three ovules. In *none* of these could be discovered a pollen-tube, by the most careful examination, in which, by longitudinal sections and subsequent dissection with the needle, the path which the pollen-tube must have taken, down to the embryo-sac, was visibly exposed. Neither could any be found in the cavity of the ovary, outside the ovules.

In other Euphorbiaceæ, chosen for comparative investigation, whose ovaries and ovules had essentially the same structure as those of *Cælebogyne*, and presented neither more nor less difficulties than *Cælebogyne* for the discovery of the pollen-tubes in their course from the stigma to the embryo-sac, a pollen-tube was readily demonstrated in the interior of the ovules.

Notwithstanding this *absence of pollen-tubes* in *Cælebogyne*—in two-thirds of those ovules which were neither too young, nor were rendered abortive by the overpowering growth of their neighbours,—of the three ova (germ-vesicles) which were contained in each embryo-sac, sometimes all, sometimes two, and sometimes only one, were *developed into young embryos*, and the particular stages of development in the formation of the embryo were found to be perfectly in agreement with those which are passed through, in other Euphorbiaceæ, *after fecundation has taken place*.

After these observations, the idea of a hybridation in *Cælebogyne* must be given up. I think that I am rather warranted in concluding from them—with the same certainty as Von Siebold derived from the numerical proportion of the positive and negative results of his observations on the presence of spermatozoids in the eggs of worker- and drone-bees—that in *Cælebogyne* the embryo really can be developed *without a previous fecundation of the ovum*.

A testimony in favour of the correctness of this assumption is furnished by the *behaviour of the stigmas* of our *Cælebogyne*-plants, upon which the first observer of the Parthenogenesis of *Cælebogyne*, J. Smith*, very properly laid great weight.

In all plants which are regularly fertilized, in which a sufficient number of pollen-grains arrive at the stigmas of the ovary, to provide the ovules with the requisite pollen-tubes, the expansion of the ovary, which takes place simultaneously with the development of the embryo, is the signal for the decomposition of the stigmas: they wither, dry, and mostly separate from the ovary. The delivery by the cells of the stigma of the material

* Linnæan Transactions, xviii. p. 509.

necessary for the development of the pollen-tubes from the pollen-grains, brings in its train the immediate death of the former, and a *destructive action upon the stigmas* is usually ascribed to the pollen-grains. In our *Cælebogyne*, on the contrary, the stigma not only does *not* wither and dry up at the epoch in which the development of the embryo is announced by the expansion of the ovary, but it *grows and increases in size* simultaneously with the enlargement of the ovary.

We are indeed deficient here in comparative observations on the behaviour of the stigmas of individuals regularly exposed to the influence of the pollen, which hitherto could only be examined in the native country of *Cælebogyne*; and a doubt may perhaps be expressed whether we may venture to take the persistent enlargement of the stigmas of *Cælebogyne* as a *proof* that no pollen has acted upon them, or whether we may not have to do here with an exceptional peculiarity, opposed to the ordinary behaviour of plants. For the removal of this doubt, however, facts come to our aid from other quarters, facts which we have become acquainted with through a series of observations on the occurrence of Parthenogenesis in the vegetable kingdom, which we place in a second rank.

Spallanzani's observation, of the power of reproduction possessed by the *female plant of Hemp* (*Cannabis sativa*), without the cooperation of pollen, has been subjected, in the last few years, by Ch. Naudin of Paris, to repeated test-experiments, the investigations being extended at the same time to *Mercurialis annua* and *Bryonia dioica**. From all these plants he has obtained fertile seeds, *i. e. seeds containing an embryo, in spite of the exclusion of the pollen*. The plants raised from these, in *Cannabis*, were male and female: no statement is made on this point in reference to the other plants.

With regard to the results obtained in *Bryonia*, we shall not place any dependence upon them, since the specimens used in the investigations were cultivated in the open ground, and therefore could not be guarded from the influence of the pollen with all the precautions requisite in such experiments.

The female Hemp-plants were, however, raised in a detached, constantly closed chamber, so that the advent of pollen-grains, either of the same or other species, was most improbable;—I will not say it was impossible, for I will not deny to accident the pleasure of now and then intervening when we least expect it, and since we even know that ordinary door- and window-fittings can be no absolute obstacle to the entrance of pollen-

* *Bullet. de la Soc. Botan. de France*, xii. p. 754, No. 11. Paris, 1855; and *Comptes Rendus*, xliii. p. 538 (1856).

grains. The impossibility of the action of Hemp-pollen, at least, was, however, really secured by the circumstance that the period of the experiment did not coincide with the epoch of flowering of the Hemp cultivated in fields and gardens. For the absence of any abnormally developed male flowers from the plants used, we have the testimony of the eyes of Naudin and Decaisne. I owe it to Decaisne's kindness that I myself had an opportunity of seeing one of these plants. Nothing could be stranger than their appearance: the plant was just ripening its fruits; these *ripening* fruits were, however, still crowned by long feather-like *stigmas*, in which there was no trace of commencement of withering,—and this at an epoch when the ovaries of the same plants which have been exposed to the action of pollen have long lost their stigmas.

The same phenomenon was observed in plants of *Mercurialis annua*, which Thuret of Cherbourg raised in a closed chamber, excluding males, for the purpose of testing Naudin's experiments. Here also, giving not a little peculiarity to the whole habit, the highly developed fruits were still, when they had attained nearly their full size, furnished with *unwithered stigmas*, which had enlarged in proportion with the growing ovaries; while in such specimens as vegetate under regular conditions, in company with male plants, the stigmas are very transitory, and always wither and fall off when the expansion of the ovary has scarcely begun. Dissection proved that the seeds of those plants raised in closed chambers contained embryos.

This unusual and remarkable behaviour of the stigmas cannot be ascribed to any other circumstance than this,—*that they had not been exposed to the action of the pollen*; that their cells had not been called upon to give up any part of their contents for the nutrition of the tubes growing from the pollen-grains. The researches on *Cannabis* and *Mercurialis* complete the above-mentioned observation of the peculiar behaviour of the stigmas in *Cælebogyne*, in a manner calculated to remove completely any doubt that might still prevail in that case. This behaviour of the stigmas is the *surest evidence* that the exclusion of the pollen in the experiments on *Cannabis* and *Mercurialis*, and, in like manner, on *Cælebogyne*, was not merely probably but actually *complete*; and we are no longer compelled, in making certain of this, to trust to the supposed sufficiency of the artificial means of exclusion, nor to the belief in the impossibility of our eyes being deceived.

Thus, then, is proved the existence of Parthenogenesis in the vegetable kingdom.

Circumstances, unfortunately, did not allow of my giving the same negative testimony, as in the case of *Cælebogyne*, as to the
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absence of pollen-tubes in the ovaries and ovules of *Cannabis* and *Mercurialis*,—nor to institute here, as I did in that case, comparative investigations on the development of the fecundated and the virgin ova into embryos. I trust to be able to do so hereafter.

Reviewing the facts which compel us to transfer the idea of Parthenogenesis in the vegetable kingdom from the domain of chimæras into the domain of reality, we find them, briefly, as follows :—

A. We are acquainted, in the specimens of *Cœlebogyme* cultivated in Europe, with plants in which the participation of the pollen of the same plant in the production of the embryo is impossible. The participation of the pollen of any allied plant is rendered in the highest degree improbable by the absence of all signs of hybridation in the progeny.

The absence of any such participation is directly demonstrated here by microscopic investigation.

This evidence is strengthened by the behaviour of the stigmas of the ripening ovaries. Our observations on this point can of course be only one-sided, but they are rendered good testimony by the support derived from analogy.

B. In other plants (*Cannabis*, *Mercurialis*) we may acknowledge, not indeed the impossibility, but the great improbability of an action of the pollen of the same or allied plants on flowering female plants kept in closed chambers.

For the absence of such action we are still without the negative proof, derived from microscopic examination, which we must never dispense with in scientific questions. On the other hand, we have a supplementary *positive* proof of it in the behaviour of the stigmas, on which we here possess observations made on all sides and mutually corrective.

We might greatly increase the number of these cases of Parthenogenesis, if we made use of the statements for whose accuracy we might take the name of the observers as surety. But we prefer, in so important a question, in which is involved the upsetting of a physiological law which is supposed to have been just certainly established by the most recent researches,—not to advance beyond our own observations; moreover, it was not part of our plan to give a list of the cases in which Parthenogenesis had been observed, but only a statement of those in which and through which it could be *demonstrated*.

Munich, Dec. 4, 1856.